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1 **Title: Social transmission of avoidance among predators**
2 **facilitates the spread of novel prey**

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14 **Introductory paragraph:**

15 Warning signals are an effective defence strategy for aposematic prey, but only if they are
16 recognised by potential predators. If predators must eat prey to associate novel warning
17 signals with unpalatability, how can aposematic prey ever evolve? Using experiments with
18 great tits (*Parus major*) as predators, we show social transmission enhances the acquisition
19 of avoidance by a predator population. Observing another predator's disgust towards tasting
20 one novel conspicuous prey item led fewer aposematic than cryptic prey to be eaten for the
21 predator population to learn. Despite reduced personal encounters with unpalatable prey,
22 avoidance persisted and increased over subsequent trials. We then use a mathematical
23 model to show social transmission can shift the evolutionary trajectory of prey populations
24 from fixation of crypsis to fixation of aposematism more easily than previously thought.
25 Therefore, social information use by predators has the potential to have evolutionary
26 consequences across ecological communities.

27

Since the first description of aposematism over 150 years ago¹, explaining how these conspicuous warning signals evolve to protect prey in the face of hungry predators remains a challenge²⁻⁴. Aposematic displays confer little advantage until predator populations associate the prey's display with its unprofitability, and while conspicuous signals are easy to detect and facilitate rapid learning⁵, this feature also means they are often taken much more readily than cryptic prey during predator education^{5,6}. If all predators must consume novel conspicuous prey to learn, then aposematism is unlikely to evolve², and nor can it be maintained easily if immigrants or juvenile predators are naïve^{7,8}. This becomes particularly problematic when prey are lethal, as predators have no opportunity to learn from their foraging mistakes⁹. Nevertheless, aposematism is a widespread defence with multiple evolutionary origins, showing that it can establish across diverse predator-prey systems^{10,11}.

Many factors might assist aposematic phenotypes overcome this cost of conspicuousness to reach fixation in prey populations¹¹, although experiments in the lab and field suggest the puzzle is yet to be fully resolved⁴. For example, aggregating reduces attack rates endured by unpalatable prey¹², but predators still require repeated encounters with prey aggregations to learn avoidance¹² and aposematic displays are more common among non-aggregating prey³. Wariness of novel food items may confer an initial advantage for aposematic prey¹¹. However experiments demonstrate that dietary conservatism is rarely sufficient to reduce initial predation risk below that of cryptic phenotypes¹³ and social effects during foraging encourage predators to become less conservative about incorporating novel foods into their diet¹⁴. Even innate biases against common warning signals (e.g. black and yellow stripes) are insufficient to protect novel prey completely: novel aposemes suffer higher mortality overall than cryptic phenotypes¹³, perhaps because reinforcement is required for predators' initial biases to become avoidance¹⁵, and juvenile predators can show less aversion to novel prey than adults^{7,15}. Furthermore, when a

predator's nutritional state declines they increase their consumption of unpalatable prey⁴ meaning aposematic prey in the wild continue to face predation⁸, even when some of the population is educated¹⁶.

Considering the information ecology of aposematism¹⁷ may help reconcile how it evolves and persists. When encountering novel prey, predators face uncertainty about its palatability and nutritional benefit⁴ so, in theory, they should acquire as much information as possible before risking consumption^{17,18}. Previous work has focussed on predators becoming educated about warning signals through interacting with and consuming prey themselves⁴ (i.e. personal information), perhaps influenced by innate preferences and biases against colours or patterns¹⁵, or wariness of unusual foods in general¹¹. However, paying attention to the foraging behaviour of others (i.e. social information¹⁷) could provide an additional potent source of information¹⁹. Social transmission of food aversions has been demonstrated in a range of taxa: for example vervet monkeys learn to prefer palatable rather than unpalatable foods by observing educated troop members²⁰, juvenile great tits increase their avoidance of aposematic prey if they observe an adult eat an alternative²¹, and tamarin monkeys²², red-winged blackbirds²³, house sparrows²⁴, and domestic chicks²⁵ avoid foods after observing a conspecific show distress. Observing another's characteristic response to distasteful food can also increase chickens' wariness of two typical colours used by aposematic prey²⁶. However, whether social transmission facilitates the evolution and spread of novel conspicuous prey compared to an alternative phenotype²⁷ remains untested.

Here we combine experiments with a mathematical model to test if social transmission of avoidance among predators enables novel aposematic prey phenotypes to reach fixation more readily than previously assumed. We used the novel-world method^{5,28}

where naïve predators search in an artificial landscape for artificial prey (paper packets containing food) marked with novel signals that are either cryptic (they share the signal printed on the landscape) or conspicuous^{5,28}. The palatability of prey is manipulated by soaking small pieces of almond in chloroquine, a mild toxin that facilitates associative learning²⁹. This method avoids using signals that are found in a predator's current environment, or in its evolutionary past. We used great tits, *Parus major*, as our model predator because they learn from personal encounters to avoid novel artificial^{5,28} and real aposematic prey^{7,30}, and also use social information for foraging: they copy foraging locations³¹ and acquire new foraging skills from observing others in the wild³². Like many bird species³³, great tits respond to distasteful prey items by shaking their head and wiping their beak vigorously on a nearby perch (Supplementary Videos 1,3); using video playback, we provided half of the predators with this potential source of social information about signals and unpalatability before they encountered the prey population. We predicted that socially-informed predators would (i) forage for novel prey more quickly than naïve predators without social information³³, and (ii) consume fewer conspicuous than cryptic prey despite them being almost three times more visible to predators⁵. If social information is to facilitate the evolution of novel aposematic prey, avoidance must persist during multiple encounters with prey populations. Therefore, we repeated our experiment on two subsequent days (but without further video playback) and predicted that socially-informed predators would (iii) continue to avoid unpalatable prey, despite fewer opportunities for personal learning and feedback from toxin ingestion⁴. We then used a mathematical model (Box 1) to investigate the evolutionary consequences of social transmission for a spatial mosaic of prey populations.

Results:

Socially-informed predators were quicker than naïve control birds to select their first item from the prey population (effect of social information = -1.13 ± 0.24 , $\chi^2 = 20.06$, d.f. = 1, $p < 0.001$, Fig. 1a, Supplementary Table 1), and 67% ate a cryptic prey item first compared to 53% of predators naïve to the unpalatability of the conspicuous symbol (Fig. 1b, Supplementary Table 1). This suggests that socially-informed predators were not foraging more quickly simply because they had observed a conspecific, but that social information encouraged quicker decision-making. Observing another predator consume just one unpalatable prey item subsequently resulted in a 32.1% reduction in predation risk for the novel aposematic phenotype (Fig. 2): focal birds presented with social information consumed fewer aposematic prey items than the alternative cryptic form during the first trial, when compared to birds that needed to learn through trial-and-error only (Fig. 2; effect of social information = -0.65 ± 0.23 , $\chi^2 = 7.98$, d.f. = 1, $p = 0.005$; Supplementary Table 2). Adult male great tits (our demonstrators) are dominant over juveniles and females³⁴, yet conspicuous prey enjoyed similar protection from socially-informed predators regardless of the age of the observer (adult vs. juvenile observers = 0.22 ± 0.47 , $\chi^2 = 2.38$, d.f. = 1, $p = 0.63$) or if they were subordinate to the demonstrator (adult male vs. subordinate observers = 0.60 ± 0.45 , $\chi^2 = 2.03$, d.f. = 1, $p = 0.15$).

During subsequent encounters with prey populations, we found that all birds continued to learn to avoid aposematic prey (effect of trial number = -0.77 ± 0.12 , $\chi^2 = 24.00$, d.f. = 1, $p < 0.001$; Supplementary Table 2). Regardless of information available, birds improved across trials at a similar rate (information*trial number: $\chi^2 = 0.14$, d.f. = 1, $p = 0.71$) despite differences in the amounts of unpalatable prey ingested (effect of social information = -0.58 ± 0.18 , $\chi^2 = 12.13$, d.f. = 1, $p < 0.001$; Supplementary Table 2). Therefore, when experimental prey populations were under selection from socially-educated predators, the

aposematic phenotype was more likely to persist than the cryptic form, even across subsequent days (Fig. 2).

Our experiments provided ample opportunity for socially-informed birds to also learn through personal experiences: the artificial prey population was already 50% aposematic⁵. In nature, however, the proportion of aposematic prey present will vary, which will affect the chances for observers to witness and learn from predation events. We therefore next investigated the expected evolutionary consequences of social transmission using a modelling approach (Box. 1) where we varied (i) the initial proportion of the population that was aposematic, (ii) the cost of conspicuousness, and (iii) the number of predators learning by observing a predation event, relative to the probability of learning from a single personal encounter with distasteful prey. We assumed that the predator was not a specialist on the focal prey species, and our model implicitly assumed the availability of alternative palatable prey.

The positive effect of social transmission on prey survival we detected in our experiments also made a difference, at suitable parameter settings, between whether crypsis or aposematism was selected to fixation (Fig. 3, the depicted 20% initial aposematism is above the threshold if individuals learn from others, but below it if they do not). Fixation of the aposematic phenotype required crossing a wider invasion barrier: if abandoning crypsis means prey are much more visible (high α , Fig. 4), then warning colours should be common to begin with. However, when conspicuousness (α) was higher, then the benefit conferred by social transmission was also larger (it was able to reduce the width of invasion barriers the most where these were widest, Fig. 4). As a net effect, however, the smaller reduction apparent at low α might matter more for fixation because narrower invasion barriers are as a whole more likely to be crossed.

Prey and predators occur across a spatial mosaic of meta-populations which could influence the dynamics and effects of social transmission; avoidance learning may not necessarily occur at the same rate at every site³⁵ and educated predators may also migrate among prey populations, reducing predation pressure on local prey populations³⁵. Therefore we next added migration and stochasticity to the model to investigate how social transmission influenced the chance that aposematic phenotypes would reach fixation. We found that immigration from neighbouring sites that have already crossed an invasion barrier can potentially aid a local population to cross it too (red area in Fig. 5). Spread is facilitated because prey subpopulations can now cross the invasion barrier sequentially: the first subpopulation to do so makes aposematism locally fixed, and aposematic individuals thereafter constantly spread to nearby habitats. Social transmission helps the first subpopulation to reach fixation, which then facilitates other subpopulations to also cross the barrier. Conversely, prey populations that do not enjoy social transmission of avoidance among predators have to rely on other processes³⁵ to help aposematism cross the (now higher) threshold to spread towards fixation.

Discussion:

If predators have access to social information about prey palatability and signals, our empirical and theoretical results suggest that aposematism can arise more easily: (i) social information reduces the initial frequency of aposematic prey required for predator populations to become educated, (ii) it can also have an effect even when signals are moderately conspicuous, and (iii) migration of predators and spatial assortment of prey types increases the strength of these effects. Using social information during foraging is a widespread phenomenon, from insects³⁶ to fish³⁷, reptiles³⁸ and mammals³⁹. While demonstrating that avoidance is influenced by observing the interactions of others with

unpalatable foods is limited thus far to a few species of mammals^{20,22} and birds^{21,23,26}, the cognitive processes involved in acquiring avoidance asocially are unlikely to be different from learning socially⁴⁰. This means that social information has the potential to influence how many species acquire avoidance. While our experiments used great tits as a model predator, the positive effects we detected of social transmission for novel prey phenotypes could therefore occur across a wide range of predators and prey.

Our experiments and model were conservative; we gave observers in our experiment only one opportunity to gather social information, and naïve predators could only observe others showing a disgust response once they took an aposematic prey item. Social transmission may also occur, however, if animals observe the foraging decisions of already-educated group members^{20,21}, and there is growing evidence that individuals adopt the majority foraging choices of a group^{20,32}. Furthermore, aposematic prey may sometimes survive predator attacks⁴¹. Although we did not consider this ‘taste-rejection’ in our experiments or model, tasting could potentially provide social information as well as enhance the personal learning of predators⁴¹. Rejected prey would also re-join the prey population, and therefore have potential to educate again. Field experiments recording social transmission and prey survival are required to assess if these processes occur among predator populations; if present, social information could have even stronger effects for aposematic prey in nature than what we detected here.

Is social learning necessary for social transmission of avoidance? Our experiments did not allow us to assess the exact cues used by observers to adjust their foraging decisions, so observers might have been reluctant to eat the demonstrated signal only to avoid perceived competition (all of the demonstrators used were adult males), for example. However, subordinate great tits will readily move towards a food source once a more dominant bird

has moved³⁴ and during the testing phase birds foraged alone. Alternatively, observing another encounter something unpalatable might have encouraged predators to avoid the more conspicuous option by simply increasing neophobia²⁶ or fear⁴². Our data suggests that predators did, however, associate social information with the conspicuous prey signal. “Socially-informed” predators consumed fewer aposematic prey than naïve control birds during the first day, meaning they had fewer opportunities to associate prey signals with palatability directly⁴. If social effects were the cause of the initial reduction, then predation risk should have increased during the second day of the experiment to be the same (or higher) than in the control group. We detected the opposite: socially-informed predators continued to avoid the aposematic prey more than the control group across all three days of the experiment. In addition, both cryptic and conspicuous prey signal types were novel to the birds, and during the video validation experiment focal birds chose to eat from a less preferred cup after observing a disgust response (Supplementary Fig. 1). Together this suggests that social learning is the more likely explanation, but further work is needed to pinpoint the units of information.

Social transmission of knowledge about warning signals is likely to interact with other mechanisms and conditions suggested necessary for the evolution of aposematism. Wariness of novel foods by predators, for example, could help rare aposematic phenotypes to evolve if it reduces initial attacks^{11,15}, but dietary wariness varies within predator populations¹³ and initial wariness requires negative feedback to persist². Social transmission, however, could resolve this if warier individuals learn avoidance by observing the foraging of less wary predators, instead of eventually consuming prey themselves². Social information may also be more readily available if prey are aggregated, enhancing the proposed positive effects of aggregations for the evolution of aposematism³ (Fig. 5A). Predators also aggregate and flocking among birds facilitates transmission of information about food⁴³. In addition,

flocks commonly include heterospecifics⁴⁴ who may have different propensities to try novel prey items⁷. This means that there could be local variation in the social information available to naïve predators, perhaps explaining why aposematic signals vary among predator communities⁴⁵. Furthermore, even educated predators will sometimes taste aposematic prey⁴ (Fig. 2); this too could provide local knowledge about prey signals for any naïve immigrants^{8,16}.

Our findings indicate that social interactions within species may have broad implications for understanding interactions among species⁴⁶. For example, range expansion of predators or their prey can lead to populations that are naïve to prey defences. This often has disastrous consequences, but sometimes avoidance occurs much more rapidly than expected⁴⁷. Variation in social behaviour and predators' propensity to learn by observing others could help explain why some species have been able to associate toxicity of novel prey rapidly and consequently avoid consuming them⁴⁸. Despite growing awareness that social networks influence how species learn about their environment, the emergent properties of social transmission for interacting species are only beginning to be realised^{46,49,50}. Our study demonstrates that social transmission among predators has the potential to influence the evolutionary trajectories of prey. Understanding the complexity of coevolution therefore requires an appreciation of the social dynamics taking place within, as well as between interacting parties.

Methods:

Predators and housing. Wild great tits (*Parus major*) were caught from October 2013 till January 2014 using traps at feeding stations (containing peanuts) in forest at the University of Jyväskylä Research Station, Konnevesi, Finland (62°37.7'N 026°17'E). We controlled for variation in observer-demonstrator familiarity by catching birds in groups of five, and always

within two hours (immigration and emigration rates are high during Finnish winters⁵¹). Groups always included at least one adult male (who was used as the group's demonstrator during our experiments), but used juveniles (1st year) and adults (older than 1st year), and both sexes in foraging tests. Adult males are more common in this population so we used them as demonstrators to reduce heterogeneity and because subordinate great tits are known to pay attention to the foraging behaviour of more dominant birds (adult male great tits are dominant over juveniles and females)³⁴. All birds were naïve to our experimental treatments (every great tit caught and released at the research station is ringed) and assigned alternately, but not by catching order (experimental data collected by RT).

Great tits were housed indoors in individual plywood cages (65 x 50 x 80 cm) with a daily light period of 11.5 h (lights on automatically between 8.30 and 20.00 EET). Birds had acoustic contact only. They were provided an *ad libitum* supply of fresh water, sunflower seeds, and tallow, but were food deprived prior to experiments for 2 h to ensure motivation to search for prey. Water was always available. Our experiments were conducted with permission from the Central Finland Centre for Economic Development, Transport and Environment (KESELY/1017/07.01/2010), and license from the National Animal Experiment Board (ESAVI-2010-087517Ym-23). No birds died in captivity and all were released at their site of capture following experiments.

The 'novel world' experimental arena. We used an established protocol^{5,28} to test differences in relative predation risk between cryptic and conspicuous prey signals. The floor of the aviary (3 x 3.5 m) was covered in white paper sheets, printed with 71 x 80 small black crosses and laminated to protect the surface. An additional 100 three-dimensional 'fake prey' (white paper squares with a cross symbol, 8 x 8 mm) were stuck randomly across the surface (using white double-sided adhesive foam tape). This enhanced crypsis of the prey

that shared the cross symbol (see below). The floor was divided into 8 rows using wooden planks; this allowed us to assign a grid reference to the floor so we could note where birds selected prey, and provided great tits with positions to inspect prey. Two perches were also provided on the walls of the aviary on which the birds consumed their chosen prey. The foraging choices of the birds were observed via a one-way glass window in the door to the aviary.

Artificial prey. Prey were small pieces of almond (approximately 0.1g) glued (with nontoxic UHU glue stick) inside a white paper packet (8 x 8 mm). Packets were printed on both sides with a black symbol to act as a signal of the contents. Cryptic prey were printed with a cross, conspicuous prey were printed with a square that made them 3 x more visible to the birds⁵. Conspicuous prey were made highly unpalatable by soaking the almond slices for 1 h in a solution of 30 ml water and 2 g chloroquine phosphate before air drying; great tits learn to associate signal type with prey distastefulness at this concentration²⁹.

Training procedure. Following a four-step procedure that has been described elsewhere¹³, we trained demonstrators and observers to handle our artificial prey. We used plain white packets during training, and birds could not progress to the next stage until they had opened and consumed five prey. All birds learned to open prey within one day. We next trained the birds to forage in the novel world. First, each catch-group was housed together overnight in the aviary to accustom them to the room and encourage them to forage from the floor. Sunflower seeds and peanuts were available on the floor to encourage them to forage (fresh water was always available), but plastic sheeting obscured the floor. This also ensured that observers were familiar with the demonstrator of their catch-group. The second stage of training introduced birds to the novel landscape and the presence of cryptic prey. We placed nine plain white prey in three groups, and one group of three cross-symbol prey, in

random locations. For each group, one prey item was on the wooden plank and so was highly visible, the others were on the paper background and consequently harder to find. Using three cross-type prey ensured that all birds knew how to forage in the novel world, but minimized experience with the signal. All birds were trained individually and in an identical fashion, so there were no differences among experimental treatments in their experience with artificial prey before video playback. Training was complete once birds had found and consumed all 12 prey.

Using video playback to provide social information. Video playback minimizes variation in demonstrator behaviour across replicates³³, alters foraging behavior of blue tits³³, and has been used successfully to manipulate social conditions in great tits⁵². Nevertheless, before our main experiment we validated that video playbacks lead to changes in great tits' foraging behaviour (Supplementary methods, Supplementary Fig. 1).

Before filming, demonstrators were habituated to the test chamber: a wooden box (50 cm w x 50 cm d x 67 cm h) with a tinted plexiglass front that contained one horizontal perch and fresh water at all times. The box was illuminated by a single energy-saving fluorescent light, and was placed in a dark room with no other lighting. This ensured that the demonstrator was easily observable, and could be filmed, but that the birds could not see us. Videos were recorded using an HD camcorder (Canon Legria HF R37) positioned 1 m away and centered in front of the box. After filming, demonstrators were returned to their home cages (with *ad libitum* food and water), monitored overnight, and then released back into the wild.

Demonstrators were provided with a square-symbol prey item for filming. This was placed at a ca.45° angle on the floor of the test box (by leaning it against a small piece of

adhesive putty (Blu-tack®), and was 15 x 15 mm (to enhance visibility in the video). To ensure a highly visible disgust response, and to minimize heterogeneity among demonstrators⁵³, we made the prey item as distasteful as possible by soaking the almond piece in a saturated solution of 4 g chloroquine phosphate and 30 ml of water for 1 h before being left to dry. Videos consisted of the demonstrator perching next to the prey item, before taking it in its beak to the box's perch. Here the prey was held between the perch and the bird's foot while the packet was opened, allowing a good view of the prey and its symbol. Upon tasting the almond piece, most birds dropped it before wiping their beaks vigorously (Supplementary Video 3). We then edited the videos (using iMovie version 10.0) to include 1 min 30 s of the demonstrator investigating the prey, attempting to consume it, and beak wiping (median beak wipes = 39.5, range = 17 – 59); the beginning and end of the video was spliced with a 30 s clip of the cross-symbol prey (but with no demonstrator present). This ensured that any avoidance or attraction to the cryptic prey was not because of either neophobia or neophilia. See Supplementary Videos 3 and 4 for examples.

Predation experiment protocol. Each bird was tested once per day, over three consecutive days (see Supplementary Fig. 2 for set up). Prior to our experiment, individual birds were housed for 2 h in a test box in the corner of the room, identical to that used during filming of the demonstrator, and provided with water only. The LCD monitor was positioned in front of the Perspex screen, so birds were habituated. Immediately before the first test, observers were shown a video; 15 birds in the 'socially-informed' group (4 females, 11 males; 8 adults, 7 juveniles) observed the demonstrator responding to the square prey, 15 birds in the 'naïve' control group (6 females, 9 males; 6 adults, 9 juveniles) observed a video of identical length, but with 1.5 min of each prey type without a demonstrator present (Supplementary Video 4). Our control videos included the prey to ensure that naïve and socially-informed birds were similarly experienced with the prey symbols, but did not include a demonstrator

because a bird ignoring prey may also have provided social information about unpalatability²¹.

Birds were then allowed to move into the aviary by removing the Perspex screen and controlling the lighting in the test box and in the aviary room (like most birds, great tits are immobile in the dark but move quickly towards light). We recorded when each bird left its box to explore the aviary as the start time for the experiment (there was no difference between experimental groups in their motivation to begin the experiment; $\chi^2 = 0.13$, d.f. = 1, $p = 0.72$). The novel landscape was divided into four quadrants, and 6 of each prey type were scattered randomly across each (24 cryptic prey, and 24 conspicuous prey in total, for each trial). The type of prey and its location were noted so we could ensure that we recorded the foraging choices accurately. Birds were allowed to eat 25% of prey in each trial (12 of 48 prey), and we noted the time (s), and identity of each prey item taken. A predation event was recorded if a package was opened.

Statistical analyses. We used generalized linear models with error distributions appropriate to the data structure, and included a random intercept term to account for potential variation among catch groups. There were twice as many males as females in our experiment, which precluded analyzing sex-differences in response to treatment. Analysis of the predation experiment used a binomial error distribution to model a response term where the number of aposematic prey and cryptic prey consumed were bound, and also included a random intercept and slope for each individual over the three trials. Differences in motivation and latency to take the first prey item used a negative binomial error distribution to account for skew. We ran each analysis by using Akaike's information criterion (AICc, corrected for small sample sizes) to rank a model containing the experimental treatment (in interaction with trial number where appropriate) against

candidate models that each included an additional variable of interest (date during experiment, adult vs. juvenile, latency to enter aviary, and whether individual had been used in validation experiment, Supplementary Tables 1,2) and a null model. The model with the lowest ranked AICc was retained and the significance of its terms assessed using likelihood ratio tests compared to a χ^2 distribution (model outputs in Supplementary Tables 1,2). All analyses were conducted in R version 3.4.0⁵⁴ using the lme4 package⁵⁵, and we plotted predicted values to account for effects of random terms. Supplementary Fig. 3 presents the raw data from our experiment.

Data availability:

The datasets generated during the study are available from the NERC Environmental Data Centre (<https://doi.org/10.5285/db55406b-c9a1-4a9e-88c2-2abbcb4bcad3>).

Box 1. Modelling evolutionary consequences of social transmission for prey phenotypes

We consider a population of predators and prey that inhabit either a single habitat patch (site) or several, in the latter case linked by migration of both predators and prey (see 4 below). The focal prey species has two possible morphs, palatable cryptic (C) and unpalatable aposematic (A), which are inherited from parent to offspring. We denote the population density of cryptic prey at site i at time t as $C_i(t)$ and aposematic prey as $A_i(t)$ (i and t are dropped from notation where it improves clarity). Being aposematic increases the attack rate, denoted a , by a factor α , which means that in a starting population of N predators, C cryptic prey and A aposematic prey, attacks occur at a rate $aNC + \alpha aNA$. The population dynamics are governed by the interaction of each of the following processes:

1. Naïve predators can become educated via personal experience with distasteful prey.

Predators are born naïve ($N_i(t)$) before becoming educated ($E_i(t)$); a single encounter with an aposematic prey item makes the predator educated with a probability p , and an educated predator will not touch aposematic prey again (thus it takes on average $1/p$ encounters for the transition to happen). When a proportion p of encounters with aposematic prey lead to predators leaving the state 'naïve' and arriving at the state 'educated', the total rate of individuals experiencing this transition, measured at time t , equals $p\alpha aN(t)A(t)$. If there are no naïve predators left, or if there are no aposematic prey to be encountered, no predator can become educated.

2. Naïve predators can become educated predators via social transmission.

Focal predators can observe the foraging of b other individuals who reside in the same habitat patch (cases with $b > 0$ are called social transmission scenarios). Parameter q ($0 \leq q \leq 1$) specifies the efficiency of social transmission, relative to personal experience (p). If, for example, $p = 0.5$ and $q = 0.1$, then personal experience with a distasteful item leads to

future avoidance with probability 50%, but watching another individual react the same way only leads to $qp = 0.05$ probability (i.e. 5%) that this transition happens for the observer. If $q = 1$, then watching is equally efficient as personal experiences: $qp = p$ in this case.

We make the conservative assumption that social transmission occurs only after observing others transition from naïve to educated, and observation effort is not specifically directed towards naïve individuals. The computations necessary are thus that each of these b other individuals is currently naïve with probability $N/(N+E)$, therefore each focal predator is offered ‘social transmission opportunities’ at rate $q\alpha p b N/(N+E)$, and the total number of transitions happening through social transmission is obtained by multiplying by N , the density of naïve observers capable of following this route.

3. *Prey die because of predation, and predators may also die. Both experience logistic population growth towards their carrying capacity (K_{prey} , K_{pred}).*

All attacks are assumed fatal for the prey, whether or not a predator becomes educated. Because only naïve predators attack aposematic prey, the per capita deaths of aposematic prey equal $\alpha a N$, leading to density changes $(-\alpha a N + r_{prey}(1 - (A + C)/K_{prey}))A$ for aposematic prey. The corresponding change for cryptic prey is $(-a(N + E) + r_{prey}(1 - (A + C)/K_{prey}))C$. Here r_{prey} denotes the intrinsic growth rate of the prey population and the term $(1 - (A + C)/K_{prey})$ describes density dependence leading to logistic growth where aposematic and cryptic prey are assumed to contribute identically to density dependence.

The mortality rate of predators, μ_{pred} for all predators, is assumed to be independent of whether predators are educated or not. Predator mortality may occur due to other causes than encounters with the focal prey species; and we allow for the density of naïve individuals to increase when there is turnover in the predator population (all individuals being naïve at birth). Population growth towards carrying capacity is therefore added to naïve predator density, leading to a population growth term $-\mu_{pred}N + r_{pred}(1 - (N + E)/K_{pred}))(N + E)$ for naïve predators and $-\mu_{pred}E$ for educated predators.

4. Migration.

Per capita migration rates equal m_{pred} and m_{prey} for predators and prey, respectively. Migration is assumed to lead to individuals emigrating their natal patch and landing in any other patch, which means that the net immigration for patch i , exemplified for naïve predators, is $-m_{pred}N_i + \frac{m_{pred} \sum_{i=1}^k N_i}{k}$ if there are k patches in total.

When all the processes (1)...(4) occur simultaneously, the system as a whole obeys the following equations:

$$\begin{aligned} \frac{dN_i}{dt} &= -p\alpha a N_i(t) A_i(t) - \frac{q\alpha a p b N_i(t)^2}{N_i(t) + E_i(t)} - \mu_{pred} N_i(t) + r_{pred} \left(1 - \frac{N_i(t) + E_i(t)}{K_{pred}} \right) (N_i(t) + E_i(t)) \\ &\quad - m_{pred} N_i(t) + \frac{m_{pred} \sum_{i=1}^k N_i(t)}{k} \\ \frac{dE_i}{dt} &= p\alpha a N_i(t) A_i(t) + \frac{q\alpha a p b N_i(t)^2}{N_i(t) + E_i(t)} - \mu_{pred} E_i(t) - m_{pred} E_i(t) + \frac{m_{pred} \sum_{i=1}^k E_i(t)}{k} \\ \frac{dC_i}{dt} &= -a(N_i(t) + E_i(t)) C_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) C_i(t) - m_{prey} C_i(t) + \frac{m_{prey} \sum_{i=1}^k C_i(t)}{k} \\ \frac{dA}{dt} &= -\alpha a N_i(t) A_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) A_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) C_i(t) - m_{prey} C_i(t) \\ &\quad + \frac{m_{prey} \sum_{i=1}^k C_i(t)}{k} \end{aligned}$$

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609

610 **Author contributions:**

611 RT conceived the project, and designed and conducted experiments and analyses; JM
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613 All authors wrote the manuscript.

614

615 **Competing financial interests:**

616 The authors declare no competing financial interests.

Figure legends:

Figure 1. Latency to forage and initial prey choices. **a**, Socially-informed predators foraged more quickly for **b**, their first prey item than naïve control predators. **(a)** Filled symbols show means (\pm S.E.) from a negative-binomial mixed effects GLM including a random intercept for cohort. One socially-informed predator was excluded (latency = 644 s, effect of social information with outlier included = -0.71 ± 0.36 , $\chi^2 = 3.81$, d.f. = 1, $p = 0.05$, Supplementary Table 1). **(b)** The difference in initial prey symbol taken was not significant (effect of social information on odds of predator taking cryptic prey first = 0.91 ± 0.82 , $\chi^2 = 1.34$, d.f. = 1, $p = 0.25$, Supplementary Table 1).

Figure 2. Relative predation risk for novel conspicuous prey versus the cryptic phenotype.

Mean (\pm S.E.) number of aposematic prey consumed / number expected by chance during three learning trials over consecutive days (1 trial/day). Great tits with social information about prey signals (circles, $n = 15$) consumed relatively fewer aposematic than cryptic prey, compared to birds with no social information (triangles, $n = 15$). Light-coloured symbols show individual variation in foraging choices, and the solid reference line indicates equal predation of the cryptic and aposematic prey types. Plotted data are derived from a mixed-effects binomial GLM including a random intercept for cohort, and slopes for each individual.

Figure 3. An example of the temporal dynamics predicted if social information is available.

We assume all predators are naïve at $t = 0$, aposematic prey are four times ($\alpha = 4$) easier to detect than cryptic prey, and comprise 20% of the initial prey population. When **(a)** social information is not used ($b = 0$), the proportion of naïve predators (green line) becomes less than that of educated predators (blue line), however aposematism vanishes because the former are still present and detect aposematic prey (red line) more easily than cryptic prey

(solid grey line). Conversely, **(b)** social transmission ($b > 0$) leads to a faster decline in naïve predators. Once a sufficient proportion of predators are educated, the net growth rate of the aposematic population is faster than that of their cryptic competitors, and aposematism fixes (dashed grey line). Any new naïve predators become educated almost instantly (by personal learning) because aposematic prey are now very common. Here we use $b = 5$ to demonstrate the effect (only threshold frequency varies with this value). Other parameter values: $a = 0.1$, $p = 0.2$, $q = 0.1$, $\mu_{pred} = 0.001$, $r_{prey} = 5$, $r_{pred} = 1$, $K_{prey} = 100$, $K_{pred} = 10$.

Figure 4. The threshold frequency of aposematic prey necessary for the phenotype to reach fixation. Social transmission (black circles) reduces the threshold frequency of occurrence that aposematic prey must be present for the phenotype to invade the prey population (compared to personal information only (open circles). Starting populations are created from different initial frequencies for the aposematic type (between 0 and 30%) to seek the threshold frequency that is necessary for subsequent fixation. From Fig. 3 we know that the threshold for $\alpha = 4$ must be located higher than 0.2 if there is no social transmission, and lower than 0.2 if there is; here we seek the exact threshold. Parameter values, except for α (which is now varied), are from Fig. 3.

Figure 5. The effect of social transmission on the initial population size required for aposematic prey to reach fixation. Whenever there is migration (all cases with $m > 0$), there is a range of initial population sizes (marked red) where aposematism only fixes if social transmission is possible ($b > 0$). This range of initial frequencies is higher in **(a)**, where we have ‘seeded’ five subpopulations with 100 individuals binomially chosen to be aposematic or not, than in **(b)**, where the 500 individuals ($K_{prey} = 100$ at 5 sites) were additionally grouped to form subpopulations with maximum local association of aposematic prey. Thus if, for example, an initial frequency of 0.2 led to 104 aposematic individuals, subpopulation 1

669 was assumed to be 100% aposematic, subpopulation 2 had 4 aposematic individuals (4%),
670 and the remaining subpopulations had none. Initial frequencies of aposematism ranged
671 from 0.01 to 1 but we do not show values above 0.5 as they always led to fixation,
672 regardless of the scenario. Parameter values: $\alpha = 2.5$, other parameters as in Fig. 4.